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KEY TO THE GENERA OF TILIACEAE

General characters: *trees to herbs; hairs simple and/or stellate; leaves alternate, simple, toothed, petioled, stipulate; inflorescences cymose; flowers small, regular, hypogynous, bisexual; perianth 5-merous, sepals and petals distinct; stamens numerous, sometimes in 5 antipetalous fascicles, rarely 5–10, distinct; gynoecium 2–5-carpellate, ovules many to 2 in each locule; fruit nutlike and indehiscent or capsular and loculicidally dehiscent.*

A. Plants arborescent; inflorescences small, axillary, corymb-like, cymose panicles, with a long peduncle adnate to half its length with a conspicuous wing-like bract; stamens in five antipetalous fascicles, the five innermost stamens modified into petaloid staminodia; filaments forked at apex, each branch bearing a half-anther; gynoecium 5-carpellate; fruit nutlike, smooth. . . . . 1. *Tilia*.

A. Plants suffruticose or herbaceous, woody at base; inflorescences small, minutely bracteate, short-peduncled dichasial cymes, ± opposite leaves or leafy bracts; stamens numerous, not fasciculate, rarely 5–10, all fertile; filaments not forked, the anther-halves contiguous; gynoecium 2- or 3-carpellate.

B. Cymes solitary, opposite foliage leaves; sepals unappendaged at apex; stigma conspicuous, disclike; ovary usually sessile; fruit a smooth, podlike loculicidal capsule, with many minute, irregularly shaped, truncate seeds. . . . . 2. *Corchorus*.

B. Cymes in fascicles of 2–5, opposite much reduced leaves or leaf-like bracts, appearing to form axillary and/or terminal, narrow, raceme-like panicles; each sepal with a subapical hornlike appendage; stigma inconspicuous, minutely 2- or 3-lobed; ovary and androecium on a short, glanduliferous androgynophore; fruit nutlike, globular to nearly ovoid, covered with prickles hooked at apex, few-seeded, the seeds small, ovoid. . . . . 3. *Triumfetta*.

Tribe TILIEAE [Benth.]

1. **Tilia** Linnaeus, Sp. Pl. 1: 514. 1753; Gen. Pl. ed. 5. 230. 1754.

Large deciduous trees; terminal buds aborting, the branching thus sympodial; axillary winter buds with 2 or 3 unequal bud scales; indument of simple and/or stellate hairs. Leaves 2-ranked, ovate to suborbicular-ovate, 5–25 cm. long, usually obliquely cordate to truncate at base, glabrous to densely pubescent beneath, often with tufts of whitish or brownish [rusty] hairs in the axils of lateral and/or basal veins; stipules ligulate, caducous. Inflorescences axillary, few- to many-flowered, corymb-like cymose panicles, with minute caducous bracts, manifestly peduncled, the peduncle adnate to half its length to a membranaceous, oblong to obovate, reticulate-veined, partly free winglike bract. Flowers bisexual [rarely also ♂ by abortion, the plants then polygamous], fragrant. Sepals thickish, ± boat shaped, usually stellate-hairy without, each with a transverse, nectariferous, partly hairy gland at base within. Petals longer than sepals, narrow, creamy to yellow [pinkish], imbricate. Stamens numerous, usually shorter than petals and fully developed style, in 5 antipetalous fascicles (in ours), ± cohering at base with each other within each fascicle, the innermost stamen in each group modified into a spatulate, petaloid staminode [except in some Old World species]; filaments whitish, shortly bifurcate at apex, each division bearing a dorsifixed, extrorse half-anther (1-locular at anthesis) [or filaments entire with undivided anthers]; pollen medium sized, flattened at the poles, finely subreticulate. Gynoecium usually 5-carpellate [rudimentary in ♂ flowers]; stigma 5-lobed at maturity; style elongated, slender; ovary usually 5-locular; ovules 2 in each locule, axile, slightly superposed (almost collateral), ascendent, anatropous, apotropous. Fruit dry, nutlike, with a thin, parenchymatous outer layer and a thickish, woody [or crustaceous] endocarp, subglobular [or ellipsoid to obovoid], smooth [or (4)5-ribbed longitudinally], ± tomentose [to glabrate], 1-locular by obliteration of partitions, 1(–4)-seeded. Seed obovoid; seed coat cartilaginous, brown, with a large whitish scar and short, adaxial raphe; endosperm fleshy; embryo large, "folded," the cotyledons foliaceous, cordate, palmately 5-veined and 5-lobed, somewhat plaited in the middle, revolute toward abaxial surface of seed, the radicle straight, inferior. LECTOTYPE SPECIES: *T. europaea* L.; see N. L. Britton, N. Am. Trees 684. 1908. (Classical Latin name for some European species of the genus, probably derived from Greek, *ptilon*, wing, in allusion to the winglike bract of the inflorescence.) — LINDEN, BASSWOOD.

A genus of perhaps 40 (18–65) species,[2] primarily of the North Temperate Zone, with one species reaching subarctic Europe, about nine sub-

[2] "As sharply as the genus *Tilia* is distinguished from the related groups [genera] by a number of peculiar characters, just so difficult is the classification within the genus. The number of species can not be indicated with certainty, because all species are connected with one another by transitions [transitional forms], geographic races, and numerous hybrids" (Jaccard & Frey, p. 3). (Translation supplied.)

tropical Asia, and one or two Mexico; absent from the Himalayas and Pacific North America. In eastern North America, *Tilia* occurs in rich woods from Nova Scotia, New Brunswick, and southern Quebec, southward to central Florida, and westward to central and western Texas, Oklahoma, and the eastern parts of Kansas, Nebraska, South and North Dakota, and southern Manitoba. In Mexico, the genus ranges from northern Coahuila, southward along the Sierra Madre Oriental to southern Mexico, with scattered stations in the Sierra Madre Occidental (McVaugh). There is great uncertainty regarding the number and delimitation of the species of *Tilia* within this broad range, because the characters used for distinguishing the species (e.g., presence or absence, amount, color, and type of pubescence on the lower surface of mature leaves; size, shape, and texture of leaves; and shape and size of leaf teeth) seem to be quite inconstant (apparently from frequent hybridization and introgression) and hardly of specific significance. The current tendency is to reduce the 15 species recognized in the United States by Sargent (1922) and the 14 distinguished in the southeastern United States by Bush (in Small, 1933) to four or even to one.[3] For example, Braun (1961), who recognized in Ohio three "well-marked and fairly constant species" (*T. americana* L., *T. heterophylla* Vent., and *T. floridana* (V. Engl.) Small) and a species-complex (*T. neglecta* Spach), noted: "The taxonomy of the American species of *Tilia* is much confused. No two manuals agree, either in number of species recognized or in characters and limits of species. Until detailed field studies, over the entire range of the genus in America, are undertaken to determine probable hybridization and subsequent introgression resulting from Pleistocene migrations and commingling of older species, no satisfactory treatment is possible."

In wrestling with *Tilia* in northern Florida, Kurz and Godfrey (pp. 230, 231) remark, "It is of more than passing interest that our material was subsequently borrowed by a student of *Tilia* and that individual herbarium specimens taken from separate parts of a single tree were designated by him with more than one species name . . . Granting the fact that local populations of *Tilia* in our range do exhibit, in general, degrees of difference in their over-all pattern of characteristics, we are inclined to recognize but one variable complex, *T. americana*. It seems futile to attempt segregation into more taxa, certainly not without studies applying techniques and employing values other than those traditionally used. In northern Florida, *T. americana*, thus broadly interpreted, embraces a range of plants, some of which individually correspond to *T. heterophylla*, *T. floridana* [Small], *T. crenoserrata* [Sarg.], and *T. georgiana* [Sarg.]." With specific limits so uncertain, it seems to be most reasonable at the present time to follow Kurz and Godfrey in the recognition of a single variable species, *T. americana* L., *sensu lato*, $2n = 82$, both in our area

[3] Cf. E. L. Little, U. S. Dep. Agr. Agr. Handb. **41**: 417–421. 1953; Fernald, Gray's Man. Bot. ed. 8. 999. 1950; Gleason & Cronquist, Man. Vasc. Pl. NE. U. S. Canada 461. 1963; Steyermark, Fl. Missouri 1042–1044. 1963; Brown, 1945; Kurz & Godfrey, 1962.

and the entire United States. The taxonomy of the Mexican representatives needs to be considered in conjunction with this concept.

The European *Tilia cordata* Mill., $2n = 82$, and *T. platyphyllos* Scop., $2n = 82$, and the Eurasiatic *T. petiolaris* DC., $2n = 82$, introduced into the United States, are reported to spread sometimes from cultivation to waste places and roadsides in the Northeastern States.

The flowers are pollinated mainly by Hymenoptera, especially bees, and Diptera, the insects apparently being attracted, not only by the fragrance and often bright color of the flowers, but also by the large, yellow-green bract of the inflorescence. At least in European species wind-pollination also seems to be of importance (Eisenhut). Although proterandry and the relative positions of stigmata and anthers seem to prevent self-pollination in individual flowers, pollination from neighboring flowers of the same tree is said to occur side by side with cross-pollination. As Jordan (1886) showed, the nectaries are situated at the base of the adaxial surface of the sepals, not on the petals.

The vascular ground plan shows that the androecium of *Tilia* is diplostemonous, consisting at an early stage of development of five antisepalous double groups of stamens of the outer whorl and five antipetalous stamens of the inner whorl. "As development proceeds the double group of stamens in front of each sepal separates into two half groups, with the result that in fully developed flower the whole androecium consists of five antipetalous phalanges [fascicles], each phalange [fascicle] being composed of a single antipetalous member in the centre flanked by half the antisepalous group on each side" (Saunders). Only the five originally antipetalous stamens usually are modified into staminodia.

Chromosome counts (eleven species) are $2n = 82$ and 164, suggesting that the genus is highly polyploid. Although many spontaneous hybrids are known from cultivation, and much hybridization between wild plants has been supposed, only a single wild putative hybrid, *Tilia* × *vulgaris* Hayne (*T. cordata* × *T. platyphyllos* appears to have been reported. This fully fertile hybrid is said to form pure stands in Lithuania and the Ukraine (Jaccard & Frey).

The winglike bracts promote wind transportation of the infructescences; seeds are dispersed to a lesser degree by rain wash and by some frugivorous birds and mammals, especially rodents. Under natural conditions seeds germinate slowly and irregularly, sometimes remaining dormant for two to four years. Dormancy in *Tilia americana* is due to an impermeable seed coat and a partially dormant embryo.

At least on the basis of wood anatomy, the genus has been regarded as closely allied to the Indochinese-Indonesian *Schoutenia* Korth. and *Chartocalyx* Maing. ex Mast., but these two genera have pollen of a more or less malvaceous type and seem to occupy an isolated and uncertain position in the family. The pollen of *Tilia* appears to be closer to pollen of the genera of subfam. Brownlowioideae (Benth. & Hook.) Burret than to that of the genera of subfam. Tilioideae (Erdtman, Pollen Morphol. Pl. Taxon., 1952).

Tilia americana, sensu lato, and the European *T. cordata* and *T. platyphyllos* supply highly valuable, soft, white lumber of great utility; the inner bark is sometimes used for making cordage. These and some other European and Asiatic species are cultivated as ornamentals, all being also esteemed as honey plants. Flowers of *T. cordata*, *T. platyphyllos*, and *T.* × *vulgaris* Hayne (often referred to as *T. europaea* L.) are officinal, at least in Europe. Seeds are said to be a source of oil for cooking and other purposes.

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Tribe Corchoreae Burret

2. **Corchorus** Linnaeus, Sp. Pl. 1: 529. 1753; Gen. Pl. ed. 5. 234. 1754.

Annual or perennial herbs, woody at base, or subshrubs [shrubs], usually pubescent with simple [and/or stellate] hairs. Leaves alternate, small to medium sized, usually unlobed; stipules small, linear-filiform to filiform [or lanceolate], usually caducous. Flowers small, bisexual, short pediceled to subsessile, solitary and/or in umbel-like 2- or 3[–8]-flowered sessile to short-peduncled bracteate cymes opposite the leaves; bracts small, narrow, ± persistent. Sepals usually 5, distinct, sometimes cucullate, deciduous. Petals usually 5, distinct, yellow, spatulate to obovate, sometimes short clawed, shorter [or longer] than or equaling the sepals, convolute. Disc extrastaminal, annular to cuplike, or absent (in most American species). Stamens usually numerous (rarely [5–]8 or 10), appearing ± evenly distributed, ± distinct, sometimes on a short

androgynophore; anthers introrse, dorsifixed. Gynoecium 2- or 3[–5]-carpellate; stigma large, discoid [to subglobular?], irregularly dentate, crenulate to lobulate; style simple, subcylindrical to filiform, usually longer than the stamens, with a stylar canal; ovary sessile or rarely on a short, glandless androgynophore, ± cylindrical [or subglobular], 2- or 3[–5]-locular, usually ± pubescent; ovules numerous [to 2] in each locule, usually axile in two collateral rows, ± pendulous, anatropous, epitropous [or apotropous]. Fruit a loculicidal capsule, ± cylindrical, usually elongated and podlike [or ellipsoid to subglobular], terminating in a beak, short horns, or teeth, smooth [rarely with soft, spine-shaped excrescences], glabrous or ± pubescent with simple [or stellate] hairs, 2- or 3[–5]-locular [sometimes with incomplete transverse partitions between the seeds], 2- or 3[–5]-valved [or sometimes indehiscent]. Seeds usually numerous in each locule, irregularly 3- or 4-angled or disclike, usually with truncate ends, dark brown to black; seed coat coriaceous or crustaceous, the raphe fine, hardly noticeable, oblique, apparently lateral, the chalazal knot cushion-like; endosperm fleshy; embryo large, axial, "folded"; cotyledons foliaceous, entire; radicle superior. LECTOTYPE SPECIES: *C. olitorius* L.; see Britton & Millspaugh, Bahama Fl. 262. 1920. (Name from Greek, *korkhoros*, an ancient name for some herbaceous pot plant, perhaps *C. olitorius*; etymology obscure.)

A pantropical genus of about 40 species, centered in Africa (ca. 15 species) and Australia (ca. 15 species), with several in Asia and America. Two tropical American and one pantropical species occur in our area. The American species, except the pantropical *Corchorus aestuans* L. and the East African-West Indian *C. hirsutus* L., seem to differ from those of the Old World at least in an obsolete disc in the flowers.

Corchorus siliquosus L., $2n = 28$, is a subshrub or perennial herb, with leaves only 1–3 cm. long and slender, nearly cylindrical capsules 5–8 cm. long, bearing four minute toothlike appendages at the nearly truncate apex. Occurring almost throughout tropical America, it extends northward through the West Indies to hammocks, cultivated ground, and roadsides of the Florida Keys and southernmost peninsular Florida, where it seems to be indigenous. Records from Texas need verification. *Corchorus orinocensis* HBK., usually a sparingly branched annual or perennial with slender, subcylindrical, slightly flattened capsules 4–7 cm. long and attenuated into a straight beak, is widely distributed throughout tropical America and similarly reaches southernmost Florida (Dade and Monroe counties). It is also known from Mobile and Tuscaloosa counties, Alabama, southeastern Louisiana, and from scattered localities westward through southern Texas to southern Arizona and Mexico. The Alabama occurrences (and perhaps those in Louisiana) seem to be incidental introductions with subsequent naturalization (see R. M. Harper, Geol. Surv. Ala. Bull. **53**: 152. 1944). A third species, the widely distributed *C. aestuans* L. (*C. acutangulus* Lam.), $2n = 14$, is known as an adventive weed from at least Dade, Collier, Leon, and Escambia counties, Florida,

and Mobile County, Alabama. It is usually an annual, with bristle-like appendages on the lowermost pair of teeth of the leaves, a minute androgynophore bearing a disc at the apex, and stoutish, subcylindrical, 3(–6)-angular and narrowly 3-winged capsules 1.5–2 cm. long and terminated in three usually bifid horns.

At least the cultivated *Corchorus capsularis* L., $2n = 14$, and *C. olitorius* L., $2n = 14$, are short-day plants. The flowers of the two open respectively about an hour after and an hour before sunrise (Kundu). Cross-pollination by insects seems to be the rule, self-pollination apparently being prevented by the stigma's overtopping the stamens.

The inner, antisepalous whorl of stamens is completely suppressed, while the outer, antipetalous whorl is multiplied. The traces for the antipetalous stamens, which arise conjointly with those of the petals, divide primarily into three bundles: a median and two laterals. According to Rao, all three branch to form a large number of staminal bundles. The extrastaminal nectariferous disc (and sometimes an androgynophore) is present in the Old World species, but both seem to be absent (obsolete) in those indigenous to the New World. The stamens in a flower usually are distinct, appearing evenly distributed upon the receptacle, but sometimes a few groups of two to four stamens with filaments connate for various lengths can be observed. The anthers are dorsifixed (not basifixed, as stated by some authors) and are usually vertical and nearly straight. The orientation of the ovules should be investigated, since both epitropy and apotropy have been recorded by various authors.

Chromosome counts made for 12 species are $2n = 14$ and 28 (three species). Although no conclusions can be drawn, it is notable that two of the tetraploids are American and one is Australian, while all the diploids are either Asiatic or African. A trisomic mutant showing "dimorphic gametes" (microspores?) with $n = 7$ and 8, and an aberrant trisomic branch ($2n = 15$) of a normal diploid plant have been recorded in *Corchorus capsularis*. Hypo- and hyperploidy have also been detected in all Indian species of the genus. Numerous attempts to produce artificial interspecific hybrids, especially between *C. olitorius* and *C. capsularis*, have been unsuccessful with both diploids and induced tetraploids. In 1960, Islam and Rashid reported the first sucessful cross, *C. olitorius* ♀ × *C. capsularis* ♂, resulting in a few slow-growing, somewhat fertile hybrids. Chaudhuri and Jabbar Mia later published on successful crosses at the diploid level between *C. olitorius* and *C. capsularis* and the latter and *C. trilocularis*. These crosses resulted in vigorous and fertile hybrids, but *C. capsularis* ♀ × *C. trilocularis* ♂, on the tetraploid level, resulted in sterile hybrids. All crosses of *C. aestuans* with these species were unsuccessful.

The minute, very light seeds of *Corchorus* apparently can be distributed by wind (Islam & Khan), but the wide, even pantropical, distribution of some species seems to be due largely to casual introductions (e.g., in ballast).

The genus occupies an isolated position in the Tiliaceae, representing a tribe of its own. A revision of the genus is very desirable.

The Indo-Burmese *Corchorus capsularis* and the presumably African *C. olitorius* are important economic plants, the main source of the commercial fiber jute. Grown extensively in India and East Pakistan, and to a minor extent in the Philippines, Formosa, Brazil, and elsewhere, both often become naturalized. Leaves or young shoots of these and some other wild species are eaten as vegetables and/or used in folk medicine in many tropical countries. *Corchorus olitorius* has been cultivated as a pot herb in the eastern Mediterranean, particularly in Egypt, from ancient times. Seeds of *C. capsularis*, *C. olitorius*, and some other species are poisonous, containing glycosides of the *Digitalis* type.

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Tribe TRIUMFETTEAE Burret

3. **Triumfetta** Linnaeus, Sp. Pl. 1: 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Annual or perennial herbs, ± woody at base, or subshrubs [deciduous shrubs or small trees], ± pubescent with simple and stellate [rarely peltate] hairs. Leaves alternate, undivided and/or palmately 3[–5]-lobed, a few teeth at base of blade usually modified into glands; stipules small, linear-lanceolate, subpersistent. Inflorescences [solitary or] fascicled, short-peduncled, bracteate few-flowered umbel-like cymes (dichasia), lateral to and/or opposite the leaves or leafy bracts and sometimes also terminal, often forming narrow, raceme-like, interrupted cymose panicles by reduction of leaves. Flowers distinctly pediceled, usually small, bisexual [sometimes also carpellate, the plants then polygamodioecious]. Sepals 5, distinct, narrow, ± flat or cucullate, abaxially ± pubescent with simple and stellate [rarely peltate] hairs and each with an abaxial subapical hornlike appendage. Petals 5 [or absent], distinct, yellow, narrow, equaling to shorter than sepals, with a transverse band of stellate hairs on the adaxial (interior) surface above the short claw and a thickened glandular (?) area at the base, imbricate. Androgynophore usually present, short, bearing 5 antipetalous glands on its surface and often a thinnish, ciliate extrastaminal disc at its apex. Stamens numerous to 5 [3], inserted at apex of androgynophore, distinct [staminodial or absent in ♀ flowers], usually shorter than the style; anthers introrse, elliptic in outline, dorsifixed. Gynoecium 2- or 3[–5]-carpellate; stigma minutely 2- or 3-lobed [or unlobed], the lobes short, filiform, spreading; style long, slender, solid; ovary 2- or 3[–5]-locular, densely covered with minute tubercles, each terminated in a hyaline incurved [or erect] spinule; ovules 2, collateral in each locule, pendulous from the top of axile placentae, anatropous, epitropous. Fruit indehiscent, nutlike [or dehiscent, capsular or schizocarpous?], small, globular or ovoid, 2- or 3[–5]-locular, sometimes appearing either 4- to 6[–10]-locular through development of false partitions between the seeds or 1-locular by reduction of one or more locules; surface covered with spreading or ± upright, subcylindric-subulate, rigid, [glabrous or]

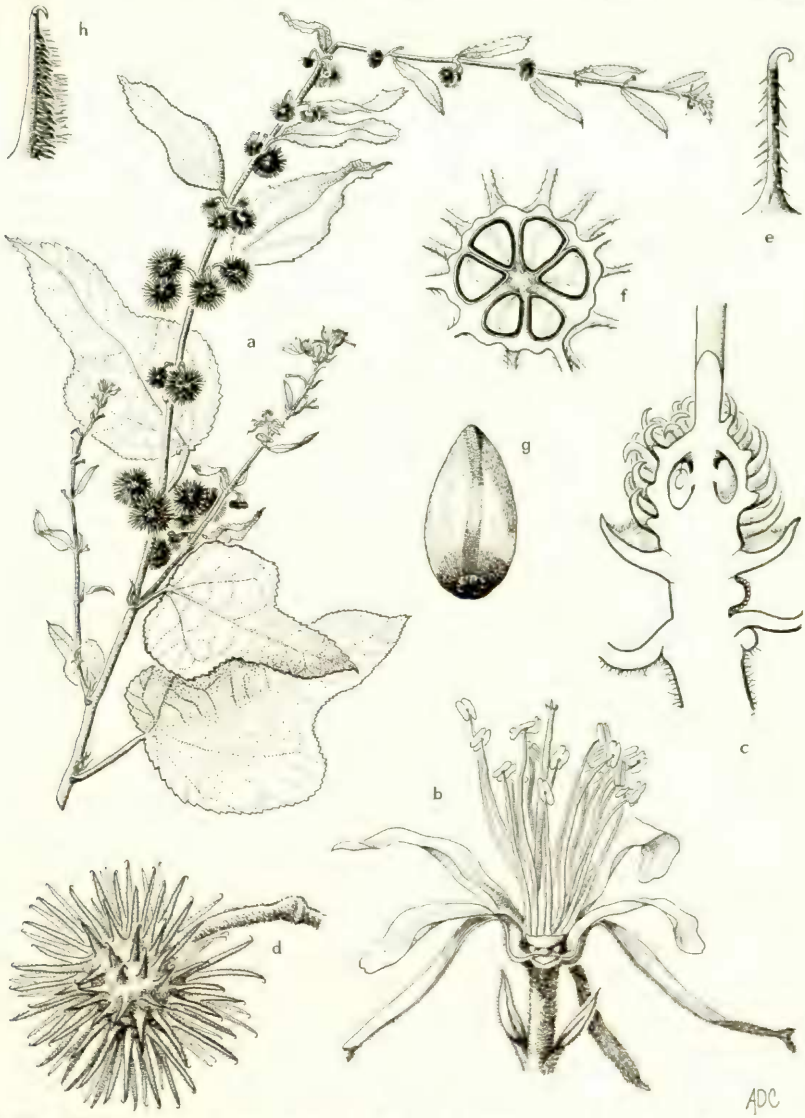

FIG. 1. **Triumfetta.** a–g, *T. semitriloba:* a, upper part of stem in flower and fruit, × 1; b, flower (two sepals, one petal removed), showing short androgynophore with three of the five antipetalous glands, disc, stamens, and style with 3-lobed stigma, × 12; c, flower in semidiagrammatic vertical section (stamens removed), to show androgynophore with a gland, disc, and anatropous ovules (one in section) with obturator of hairs, × 40; d, fruit, × 6; e, fruit prickle, × 12; f, fruit in semidiagrammatic cross section, showing two 2-seeded locules and thin false partition between seeds in the third (lowermost), the cotyledons outlined in dots, the sclerified part of seed coat in black, × 8; g, seed with circular chalazal knot depressed in center, membranaceous outer layer of seed coat obliterated, × 16. h, *T. pentandra:* fruit prickle, × 12.

retrorsely hispidulous or plumosely pubescent prickles, each usually terminated by one [to several] stiff, clawlike [or ± straight] hyaline spinules. Seeds (1) 2–6[–10], ovoid [lenticular or subreniform?], with a fine, linear, adaxial raphe (usually obliterated on mature seeds) and a basal, circular, depressed chalazal knot; outer seed coat thin, membranaceous, the inner coriaceous to crustaceous; endosperm fleshy; embryo large, axial, straight, "spatulate," the cotyledons flat, ovate to suborbicular, the radicle superior. TYPE SPECIES: *T. Lappula* L. (Name commemorating Giovanni Battista Trionfetti, 1658–1708, professor of botany at the University and director of the Botanical Garden in Rome.)

A pantropical genus of over 100 species, apparently almost equally centered in tropical America and Africa, less abundant in Asia, Australia, and the Pacific Islands. At least four species, two naturalized in the southernmost part of our area, are of pantropical distribution. Sprague and Hutchinson recognized four sections based primarily on fruit characters. All American and most Old World species belong to sect. TRIUMFETTA (§ *Lappula* DC. em. Sprague & Hutch.).

Triumfetta semitriloba Jacq., $2n = 32$, occurs in cultivated ground, hammocks, and pinelands on the Florida Keys and in peninsular Florida, north at least to Manatee County, on the west coast, and Palm Beach County, on the east. It is a perennial herb or subshrub, with variable, generally ovate, unlobed to 3-lobed leaves; flowers with flat sepals, a well-developed disc, and 15–25 stamens; and nearly globular, subglabrous fruits with sparsely retrorsely hispidulous prickles. In contrast, *T. pentandra* A. Rich. is an annual or perennial herb with broadly ovate, unlobed to deeply 3-lobed leaves sparsely pubescent with simple and stellate hairs; flowers with cucullate sepals, a somewhat reduced to obsolete disc, and 5–8 (13) stamens; and subglobular-ovoid fruits with ± upright prickles plumosely pubescent on the adaxial side with straightish spreading hairs. It was collected in Sumter County, Florida, in 1900, but present status in our flora is uncertain.[4] Although apparently pantropical, the species seems to be most abundant in Africa and rather scattered and local elsewhere (Cape Verde Islands, Arabia, India, Ceylon, Formosa, Timor, and northeastern Brazil).

Cross-pollination by insects seems to be the rule, selfing apparently being prevented, at least in many species, by the position of the stigma

[4] Small (Man. p. 842. 1933) and Lay (p. 383) considered this species to be *Triumfetta rhomboidea* Jacq. (*T. Bartramia* L., nom. illeg.), $2n = 32$ and 48, a pantropical species rather common in tropical America. Their opinion, if based on the single collection cited by Lay, *Curtiss 6738* ("Found in great abundance [growing 5 or 6 feet high] in cultivated ground at Webster, Sumter Co., Florida. October 27, 1900"), is apparently the result of either misidentification or misinterpretation of the species involved. *Triumfetta pentandra* A. Rich., 1830 (*T. neglecta* Wight & Arn., 1834; *T. cuneata* Hochst. ex A. Rich., 1847; *T. Sampaioi* Monteiro, 1938), is very similar and closely related to *T. rhomboidea*, which differs mainly in the well-developed disc, (8) 10–15 stamens, and nearly globular fruits with spreading, glabrous or subglabrous prickles. The Curtiss collection is clearly *T. pentandra*.

above the stamens. Data on pollinators are scarce, but bees, little beetles, and flies are recorded for some Old World species. The flowers of *Triumfetta flavescens* A. Rich. open at about 3 P.M. [Ethiopia] and those of *T. macrophylla* K. Schum. toward evening [East Africa]. "It is probable that the flowers of other species of *Triumfetta* open late in the day" (Sprague and Hutchinson).

The inner, antisepalous whorl of stamens in the flowers is completely suppressed. The trace for each of the outer, antipetalous stamens arises conjointly with a petal trace and then divides into three bundles, a median and two laterals, as in *Corchorus*. However, in *Triumfetta*, the median bundle remains adnate to the petal trace and feeds only a "staminodial nectary." The laterals usually undergo a secondary branching in connection with the multiplication of the stamens, each lateral giving rise to traces to two or more stamens (Rao, 1952). Flowers with a low number of stamens have not been investigated.

An obturator, consisting of unicellular hairs, recorded by Rao & Rao for *Triumfetta rhomboidea*, is also present in *T. semitriloba*.

Chromosome counts have been made for three species ($2n = 32, 48$). Occurrence of both 32 and 48 in *Triumfetta rhomboidea* suggests that the basic chromosome number of the genus is 8, rather than 16 as suggested by counts of $2n = 32$.

Fruits in *Triumfetta* are either dehiscent and capsular to schizocarpous or indehiscent and nutlike at maturity, but often (perhaps always?) splitting and freeing the seeds as the pericarp and partitions decay. Precise data on fruit dehiscence seem to be lacking; both loculicidal dehiscence and splitting into carpels or cocci are mentioned by various authors. The clinging fruit of species of sect. TRIUMFETTA, with their hooked prickles, are dispersed by man and other animals. In the species with densely plumose-pubescent, bristle-like fruit prickles (sect. LASIOTHRIX Sprague & Hutch.), dissemination by wind may be assumed, while in some creeping, Indo-Pacific littoral species with fruits equipped with narrowly conical nonhooked prickles (sect. PORPA (Blume) Sprague & Hutch.), dispersal by sea on floating pumice and on drifting logs has been recorded. The pantropical distribution of some species seems to be due mainly to human agency.

The genus is closely related to *Heliocarpus* L., a tropical American genus centered in southern Mexico and Central America. A revision of the entire genus is desirable.

Some species (e.g., *Triumfetta rhomboidea*, *T. semitriloba*, *T. Lappula*, *T. cordifolia* A. Rich.) yield fibers used locally in tropical countries for cordage, as well as for many domestic purposes; fibers from *T. rhomboidea* are said to be of commercial value. Leaves of several species are used as vegetables and also find some application in folk medicine. *Triumfetta rhomboidea* is said by Wilczek to be a remedy for leprosy.

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ELAEOCARPACEAE A. P. de Candolle, Prodr. **1:** 519. 1824, "Elaeocarpeae," nom. cons.

(ELAEOCARPUS FAMILY)

Trees or shrubs, differing from Tiliaceae mainly in the absence of mucilage cavities and ducts (although mucilage cells occasionally occur in the epidermis of leaves), in the considerably smaller spheroid to prolate pollen, and in the more primitive wood structure. Additional distinguishing characters include the occurrence of opposite leaves in some or all species of some genera, the prevalence of valvate petals and apical dehiscence of the anthers, and the nearly regular occurrence of a nectariferous (extra- to intrastaminal) disc. TYPE GENUS: *Elaeocarpus* L.

A nearly pantropical family of about ten genera and 400 species, centered in Papuasia (five genera, ca. 190 species) and South America (five genera, ca. 70 species), with a few extensions into the South Temperate Zone; absent from continental Africa. The single species of *Muntingia* is becoming naturalized in southernmost Florida.

Similarities in floral structure with Tiliaceae suggest a like floral biology and pollination by insects. Data from floral anatomy and embryology are few. Recorded chromosome counts (two genera, seven species) are $2n = 24, 28, 30$, suggesting aneuploidy. The petiolar anatomy appears to be more complex than in Tiliaceae.

The family is closely related to and sometimes included in Tiliaceae, but evidence from anatomy and palynology seems to be in favor of retaining the Elaeocarpaceae as a separate family. A relationship to Flacourtiaceae-Prockieae has also been postulated by some authors.

Some species of a few genera yield tanbark or lumber of local importance. A few species of *Aristotelia* L'Hérit., *Crinodendron* Mol., and *Elaeocarpus* are grown as ornamentals in the southern part of our area and/or southern California.

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1. **Muntingia** Linnaeus, Sp. Pl. 1: 509. 1753; Gen. Pl. ed. 5. 225. 1754.

Shrubs to small trees pubescent with simple and stellate hairs and viscid articulated trichomes; nodes 3-lacunar. Leaves 2-ranked, membranaceous, 3-nerved at the very oblique semicordate base, with 3–5 veins on each side of the midrib, closely to remotely toothed, villous with stellate hairs and cobwebby beneath, short petioled, with a single ± lateral filiform stipule (the second wanting or rudimentary?). Flowers regular, 1.5–3 cm. in diameter, hypogynous, usually supra-axillary, long pediceled, either solitary or in sessile (or rarely short-peduncled) fascicles of 2 or 3, with 3 filiform bracts at base. Sepals 5(–7), ± lanceolate, caudate, the filiform tip almost equaling the blade, connate at the very base into an in-

conspicuous shallow saucer-like calyx tube, densely pubescent on both surfaces, valvate. Petals 5(–7), distinct, white (rarely pink), thin, obovate, short clawed, equaling the sepals, imbricate and ± crumpled in bud. Disc intrastaminal, annular, on the edge of the shallowly concave receptacle, bearing a ring of long, straight hairs on the exterior side near the margin. Stamens numerous, distinct, inserted at base and partly on the exterior surface of disc, half as long as the petals; filaments filiform; anthers elliptic in outline, shorter than the filaments, dorsifixed, versatile, introrse (latrorse), longitudinally dehiscent. Gynoecium 5–7-carpellate, syncarpous; stigma subsessile or sessile, subpyramidal, longitudinally 5–7-grooved and -ridged, with a sinuous stigmatic surface on each ridge; style very stout and short or wanting; ovary sessile or very short stalked, 5–7-locular, the locules becoming slitlike, pubescent, and confluent above the placentae; ovules very numerous, anatropous, epitropous, on 2 ± ovoid placentae pendulous from the axis at the top of each locule. Fruit a subglobular berry, ca. 1 cm. in diameter, red or yellow, appearing irregularly many-locular, sweet, edible. Seeds numerous, obovoid to ellipsoid, minute; seed coat crustaceous, the cells of outer epidermis mucilaginous; raphe indistinct, the chalazal knot apiculate; embryo axial, stout, straight, subcylindrical, the cotyledons small, semicircular in cross section, nearly equaling the thick superior radicle. TYPE SPECIES: *M. Calabura* L. (Name commemorating Abraham Munting, 1626–1683, professor of botany in Groningen, Nederland, and author of several botanical works.)

The single species, *Muntingia Calabura*, widely distributed in the West Indies and from southern Mexico to Peru, northern Argentina, and Brazil, has become established in pinelands and hammocks (e.g., Sisal Hammock) in Dade and Hendry counties, Florida. Its further spread seems likely, for the ability to reproduce vegetatively and a tendency to become weedy have been recorded for the species.

The solitary flowers or fascicles of two or three flowers which develop in a sequence are derivable from the simple, peduncled dichasia which are sometimes encountered in the species. The floral anatomy, in general, is similar to that in Tiliaceae and in *Elaeocarpus* (Rao). The lack of one stipule seems to be correlated with the absence of one stipular trace (Sensarma).

The taxonomic position of *Muntingia* is uncertain. The embryo development is of the Onagrad type, which seems to be otherwise unknown in the Malvales. The smaller pollen and the absence of mucilage cavities in the axis and leaves suggest that it should be retained in the Elaeocarpaceae. However, the microscopic structure of the wood differs from that of the other genera of Elaeocarpaceae, but is very similar to that in *Dicraspidia* Standl. and has many points in common with other Tiliaceae (Metcalfe & Chalk). The structure of the leaf and inner bark, resembling that in *Tilia* (cf. Dumont), also seems to indicate a closer relationship to Tiliaceae than to Elaeocarpaceae. The genus is undoubtedly closely related to the

monotypic *Dicraspidia* (*D. Donnell-Smithii* Standl.), which is known from Honduras, Costa Rica, Panama, and Colombia.[5]

Grown as an ornamental in many tropical and subtropical countries, *Muntingia Calabura* often becomes naturalized. Fibers from the inner bark are used locally for making cordage and in basketry.

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STANDLEY, P. Studies on American plants — I. Publ. Field Mus. Bot. **4**: 197–299. 1929. [*Dicraspidia* Standl., 226–228; relationship with *Muntingia*, 228.]

[5] After having established *Dicraspidia*, Standley (p. 228) wrote, "There is no doubt in the writer's mind, however, that the plant is closely related to the genus *Muntingia*, and that it should be referred, consequently, to the Elaeocarpaceae, or rather to Tiliaceae, if these families are to be combined. In general aspect, and in pubescence, leaf form, and gross appearance of the flower *Muntingia* and *Dicraspidia* are very similar, so much so that their relationship can scarcely be questioned." Metcalfe & Chalk (p. 265) noted the similarity of the two in wood structure, which is different from that of the rest of the Elaeocarpaceae. *Dicraspidia*, in turn, doubtless is closely related to the monotypic eastern Peruvian *Neotessmannia* Burret, the single member of Tiliaceae subfam. Neotessmannioideae. *Muntingia* with its hypogynous flowers, on the one hand, and *Dicraspidia* and *Neotessmannia* with epigynous flowers, on the other, agree in many characters, especially in the supra-axillary position of the flowers and peculiar stigmata not encountered elsewhere within the Malvales. The three seem to form a special line of evolution either within or parallel to Tiliaceae. That these genera are monotypic seems to indicate the antiquity of the group.

POLLEN OF DEGENERIA VITIENSIS

A. ORVILLE DAHL [1] AND JOHN R. ROWLEY [2]

SINCE THE ORIGINAL DESCRIPTION of the uncommon, monotypic genus *Degeneria* of the family Degeneriaceae by Bailey and Smith (1942), additional collections of flowering and fruiting material throughout its known range in Fiji have been made by Smith (1949). Swamy (1949), in his careful morphological analysis of the family, included a description of the microsporangium and microspores derived from Dr. Smith's collections.

This paper is a summary of additional observations made on microspore and pollen material utilizing primarily the techniques of phase contrast microscopy in association with electron microscopy.

MATERIALS AND METHODS

All observations were based on preparations made from specimens collected and preserved in Fiji by Dr. A. C. Smith. The field collections available for use were Dr. Smith's numbers *5744*, *5875*, and *5880*. The reagents used for fixation were limited to formalin-acetic acid-alcohol (FAA) and, in one instance, to potable spirit (gin). Despite the poor over-all state of preservation for purposes of electron microscopy, data on our preparations are reported in view of the present scarcity of material.

Microspores and mature intact pollen grains were mounted from the preservative into various media (cf. Bailey, 1960; Dahl, 1952). Precise, but impermanent, staining of pectic components of apertural membranes was attained by mounting the specimens in filtered 0.2% ruthenium red in 75% aqueous glycerine (Mangin, 1893; Bailey, 1960). The slides retained specificity of reaction for a period of up to ten days when stored in a refrigerator.

Material was mounted, either directly or after extracting procedures, in lactic acid (ca. 85%) or media based largely on this reagent (e.g., "lactic-iodine" made by combining 1 part of 1% iodine and 1% potassium iodide in 80% ethanol with 3 parts of lactic acid, or "lactic-triacetin"

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[2] During early phases of this study, space and equipment were generously provided by Professor A. Frey-Wyssling and Professor K. Mühlethaler, Swiss Federal Institute of Technology, Zürich.

composed of 4 parts lactic acid and 1 part triacetin, or "lactic-butanol" prepared by combining 4 parts of lactic acid with 1 part of *n*-butanol). Such non-hardening media require sealing of the cover glass with a relatively inert varnish such as the phenolic "Tuf-On" #74 varnish (obtained from Brooklyn Paint & Varnish Co., Inc., 50 Jay St., Brooklyn 1, N.Y.). Preparations that did not require sealing were obtained by mounting the material in a variation of Downs' (1943) polyvinyl-lactophenol mixture designed to attain much of the favorable optical characteristics of lactic acid. This variation is made up of 3 parts lactic acid, 2 parts 15% aqueous polyvinyl alcohol (medium viscosity), and 1 part phenol.

Pollen grains badly darkened by the preserving fluid were partially cleared when mounted in 70% aqueous chloral hydrate. Such mounts were satisfactory for phase contrast analysis.

A desirable optical environment for purposes of phase contrast analysis of sections of methacrylate-embedded specimens with the embedding medium still present was maintained by mounting the sections in a drop of a 1:1 mixture of poppyseed oil and *n*-butanol followed by sealing of the cover glass. For ordinary microscopy, similar sections of methacrylate-embedded microspores were mounted in the lactic acid-iodine medium. After sealing, these preparations revealed the familiar yellow-stained cell walls and purple-stained starch grains in an optically suitable environment.

Pollen grains were treated with Novopokrowsky's (McLean & Cook, 1952) chloroiodide of zinc for observation of apertural structures.

Microscopical observations were made with apochromatic (Leitz, N.A. 1.32) and fluorite phase (Leitz, N.A. 1.15 and Wild, N.A. 1.30) objectives.

Electron microscope preparations were obtained from osmium tetroxide, potassium permanganate, and uranyl acetate-stained materials (Pease, 1960) embedded in methacrylate or the polyester copolymer "Vestopal W" (Ryter & Kellenberger, 1958).

OBSERVATIONS

Microspore Stages. During the quartet stage of telophase II of meiosis, a callose wall up to ca. 2.5 μ in thickness bounded each group of microspore protoplasts. The early microspores in the available quartet stages did not have an exine.

The youngest available microspores (Fig. 1) bounded by exine were at a pre-mitosis stage. The exine was fully developed and continuous over the entire microspore surface. The outer surface of the exine was smooth while the inner surface was fimbrillate (Figs. 5–7). An incipient aperture was differentiated but not expanded. In thin sections, the exine was found to taper gradually in thickness as it extended from proximal regions of the pollen grain to the apertural margin where exine of minimal thickness occurred (Fig. 5). Over the incipient germinal aperture, the exine was undulate and was 3 to 5 times thinner than in nonapertural regions (Figs. 8 & 9). Intact microspores at this stage were about 40 to 44 μ in diameter with a perimeter of 125 to 135 μ (Fig. 1).